Freezing Behavior of Potato (*Solanum tuberosum*) Tubers in Soil

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ABSTRACT

Volunteer potatoes are a major weed problem in potato rotations in regions with mild winter soil temperatures. Freezing dynamics of potato tubers in air have been previously reported, but freezing dynamics of tubers in soil may differ due to ice nucleation sites and soil water associated with soil. Laboratory experiments conducted in hydrated and dry soil columns and field experiments were conducted to determine cold temperatures required to kill potato tubers in soil. Potato tubers in air-dried soil columns exposed to decreasing temperatures typically supercooled to –3 to –7 C before exhibiting a distinct exotherm, which stabilized at –1.4 to –1.5 C, representing the freezing point of tubers. Tubers that were supercooled and removed from the cold environment before experiencing this exotherm were able to sprout and had no visual symptoms of freezing injury, whereas tubers that experienced the exotherm were nonviable and unable to sprout. Tubers in soil columns hydrated to 7% SWC supercooled much less than tubers in dry soil and exhibited an exotherm that stabilized near –1.9 C. Tubers exposed to temperatures near the tuber-freezing point (–1.4 to –1.9 C) for periods of 1 min to 24 h, but not undergoing an exotherm, exhibited varying degrees of injury, which increased with time of exposure. Tubers held at –1.0 C for 4 to 24 h were unharmed and able to sprout similar to controls. In field trials conducted from 1993 to 1999 in the Columbia Basin of Washington, tubers buried at shallow depths (5 cm) were much more likely to experience lethal cold temperatures than tubers buried deeper. In general, when minimum soil temperature at tuber depth reached –1.5 to –1.9 C or lower, some tuber mortality occurred and when soil temperature at tuber depth reached –2.8 C or lower, extensive tuber death occurred. Monitoring of winter soil temperatures by depth in potato- growing regions could be used to predict severity of volunteer potato for the subsequent growing season.

RESUMEN

Las plantas voluntarias constituyen un problema mayor de malezas en las rotaciones de papa, en regiones con temperaturas moderadas de suelo durante el invierno. La dinámica de congelamiento al aire de los tubérculos ha sido reportada previamente, pero la dinámica de congelamiento de los tubérculos en el suelo puede ser diferente debido a los lugares de concentración de hielo y de agua asociada con el suelo. Se realizaron experimentos de laboratorio en columnas de suelo seco e hidratado y experimentos en campo para determinar las temperaturas requeridas para matar los tubérculos de papa en el suelo. Los tubérculos de papa en columnas de suelo secado al aire expuestos a temperaturas típicamente decrecientes, enfriados a –3 hasta –7 antes de que mostraran exotermia visible, la cual estabilizada a 1.4 y 1.5 representa el punto de congelación de los tubérculos. Los tubérculos que fueran superenfriados y sacados del ambiente frío, fueron capaces de brotar y no presentaron síntomas visuales de daño por congelamiento, mientras que los tubérculos que experimentaron exotermia no estaban viables y por tanto no fueron capaces de brotar. Los tubérculos en columnas de suelo hidratadas al 7% SWC mucho menos superenfriados que los tubérculos en suelo seco exhibieron una exotermia que se estabilizó cerca de –1.9 C. Los tubérculos expuestos a una temperatura cercana al punto de congelamiento

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ADDITIONAL KEY WORDS: cold temperature, freezing point, freezing injury, groundkeepers, volunteer potato

ABBREVIATIONS: SLE, special limit of error; SWC, soil water content

(–1.4 a –1.9 C) por periodos de 1 min a 24 h, pero que no experimentaron exotermia, exhibieron varios grados de daño, que se intensificó con el tiempo de exposición. Los tubérculos mantenidos a –1.0 por 4 a 24 h no sufrieron daños y fueron capaces de brotar igual que los controles. En pruebas de campo realizadas de 1993 a 1999 en la cuenca de Columbia, Washington, los tubérculos enterrados superficialmente (5cm) estuvieron posiblemente mas expuestos a temperaturas frías letales que los tubérculos enterrados profundamente. En general, cuando la temperatura mínima del suelo llegó de –1.5 a –1.9 C o menores ocurrió alguna muerte de tubérculos y cuando la temperatura del suelo alcanzó por debajo de –2.8 C se produjo muerte masiva de los tubérculos. El monitoreo de la temperatura del suelo en invierno, por profundidades, en las regiones de cultivo de papa, podría ser utilizado para predecir la severidad de presencia de papas voluntarias en la siguiente época de cultivo.

INTRODUCTION

Potato (*Solanum tuberosum*) tubers left in the field after harvest can become a serious problem in the production of subsequent rotational crops. Field leavings of up to 460,000 and 370,000 tubers ha^{-1} have been reported in the Netherlands and the U.K., respectively (Lumkes 1974; Lutman 1977). Researchers in south-central Washington have reported after-harvest field leavings up to 454,000 tubers ha^{-1} (Newberry and Thornton 1999). Post-harvest field leavings represent increases of nine to 11 times the normal potato planting rate (Askew 1993).

Volunteer potatoes are important perennial weeds in many potato production areas. In commercial and seed potato crops, volunteer potatoes can cause rejection for certification and contamination between cultivars (Lumkes 1974; Ogilvy et al. 1989). Volunteer potatoes are hosts for Colorado potato beetle, green peach aphid, *Potato leafroll virus*, and other diseases, and they lower the yield and value of rotational crops (Askew 1991; Boydston 2001, 2004; Boydston and Seymour 2002; Ellis 1992; Lutman 1977; Thomas et al. 1997; Thomas and Smith 1983; Wright 1981). Volunteer plants are hosts for the *Paratrichodorus allius* nematode that transmits *Tobacco rattle virus*, the causal agent of corky ringspot disease, and they are also sources of late blight (Mojtahedi et al. 2003; Zwankhuizen et al. 1998). Potato shoots emerging from overwintering tubers grow rapidly in the spring, and control is difficult due in part to the tuber's ability to resprout in response to multiple control efforts (Boydston and Seymour 2002; Williams and Boydston 2002; Williams et al. 2004). As a result, managing volunteer potato can be time consuming and expensive, with costs sometimes exceeding $500 per ha in high-value rotational crops such as carrots and onions (Askew 1993; Boydston and Williams 2003; Lumkes 1974).

Potato tubers are susceptible to cold injury, and cool winter soil temperatures can kill tubers left in the soil. Plant tissues contain both intercellular water and intracellular water. Death of plant tissues from exposure to cold temperatures is usually a result of freezing of intracellular water. When water within a plant freezes it releases heat, referred to as an exotherm. The temperature at which an exotherm occurs is referred to as the nucleation temperature, and the stabilization of temperature following an exotherm represents the actual freezing point of the tissue (Proebsting and Andrews 1982). Many plant tissues are able to supercool below their freezing point without causing cell death. When tissues supercool no exotherm is observed and plant tissues are still viable if rewarmed. The formation and growth of ice crystals within a supercooled liquid must be preceded by a process known as nucleation (Ashworth 1992). Most plant tissues supercool several degrees due to a lack of nucleating substances necessary for ice initiation or to barriers to ice growth present in some tissues (Burke et al. 1976).

Early researchers conducted experiments to determine the freezing point of potato tubers in storage. They concluded that the freezing point was between –1.0 to –2.2 C, but that tubers could supercool (undercool) several degrees below their freezing point without injury (Jones et al. 1919; Link and Ramsey 1932; Maximov 1914; Muller-Thurgau 1880; Wright and Diehl 1927; Wright and Taylor 1921). Jones et al. (1919) concluded that supercooling is the normal course when potato tubers freeze. However, most research was conducted in artificial freezing chambers where tubers were not exposed to soil. Levitt (1980), citing several studies, reported the freezing point of potato tubers to fall between –0.87 to –2.0 C. Dutch researchers concluded that potato tubers are killed by exposure to 50 accumulated degree C frosts below –2.0 C (i.e., 25 h at –2.0 C, 12.5 h at –4.0 C), but that temperatures above –2.0 C had no lethal effect on tubers (Lumkes and Sijtsma 1972).

Potato tubers are able to supercool to –6.5 C under laboratory conditions where ice nucleation is prevented (Jones et al. 1919; Muller-Thurgau 1880; Wright and Diehl 1927; Wright and Taylor 1921). McKay and Clinch (1941) reported several potato tubers survived supercooling to –8.3 C. Wright and Taylor (1921) reported that wetting supercooled tubers increased freezing injury compared to tubers that were kept dry. Link and Ramsey (1932) reported that tubers with moistened surfaces only supercool slightly or not at all. Greater amounts of supercooling generally occur in plant tissues with dry surfaces as opposed to those with surface moisture (Ashworth 1992; Ashworth et al. 1985b; Burke et al. 1976; Link and Ramsey 1932; Wright and Taylor 1921). All of the mentioned studies were conducted in freezing chambers where tubers were not in contact with a soil medium. In soil, tubers are in contact with organic matter, soil water, microbes, and minerals that may act as ice nucleation sites and may affect the amount of supercooling tubers undergo. Field observations indicate that tubers do not always freeze completely, but that sometimes only portions of the tuber are injured.

Tubers left in the field following potato harvest vary greatly in size. Small tubers may be left when tubers fall through the chain of the harvester. Larger tubers are also left in fields due to inadequate harvester blade depth and spillage from harvester and trucks. Under artificial conditions lacking numerous ice nucleation sites, smaller tubers would be expected to supercool more extensively than larger tubers due to the lower number of possible nucleation sites associated with smaller surface area (Ashworth et al. 1985b; Burke et al. 1976; Fuller and Wisniewski 1998). However, Jones et al. (1919) found no relationship between tuber size and degree of supercooling of tubers in freezing chambers.

A better understanding of the freezing behavior of potato tubers and monitoring of winter soil temperatures would enable growers to accurately estimate the potential for volunteer plants prior to the growing season on a field-by-field basis. These trials were conducted to quantify the freezing injury to potato tubers in soil exposed to sub-zero temperatures above and below their freezing point. Tuber mortality, sprout viability, and sprout emergence were used to evaluate the effects of a range of symptoms of low-temperature injury and exposure events.

MATERIALS AND METHODS

Freezing Dynamics in Air-dried Soil Columns

Generation II seed tubers 'Russet Burbank' were held in a potato storage facility at 93% relative humidity and 4.5 C for 4 to 8 months prior to testing. Tubers weighing approximately 56 g were selected for studies. Soil (Quincy sand) containing 0.1% organic matter was dried at 50 C, passed through a 0.32-cm mesh screen to remove any large material, and stored at room temperature until use. Soil to a depth of 3.8 cm was added to watertight acrylic columns measuring 30 cm in height by 12 cm diameter, and a single Omega™ Type T Special Limit of Error (SLE) thermocouple, with 30-gauge wire was placed in the center of the column. A single tuber was placed on the thermocouple in the center of the column, and soil was added to the height of the center of the tuber. Four additional thermocouples were subsequently placed around the circumference of the column in contact with, but not inserted into the tuber, to avoid creation of an artificial inoculation site (Fuller and Wisniewski 1998; Wisniewski et al. 1997). More soil was added, and the final thermocouple was positioned so that it was in contact with the center of the top of the tuber and then soil added so that 6 cm of soil covered the top of the tuber. Final soil bulk density averaged 1.6 g cm^{-3}. Tubers serving as controls were held at 20 C for 24 h and then placed in a dark germination chamber at 25 C to promote sprouting.

An external bath was fabricated using a 142-L insulated cooler enclosed on all sides with 5-cm styrofoam sheets. A submersible pump was placed inside the external bath and fitted with 1.3-cm perforated copper tubing around the perimeter of the bath to aid in the circulation of coolant. Laboratory grade ethylene glycol was diluted to 50% with distilled water and added to the external bath to a depth that exceeded the soil line in the columns. A programmable NESLAB™ RTE140 low-temperature bath circulated coolant through the ethylene glycol bath, and temperature control was maintained with a remote resistance temperature detector in the external bath.

Four soil columns simultaneously were placed into the external bath that had been stabilized near –3, –4, or –5 C, and thermocouples were connected to a Campbell Scientific™ CR10 datalogger multiplexed to a Campbell Scientific™ AM416 and soil temperature data were recorded every 10 sec and averaged every minute. Average coolant temperatures were recorded each minute using two Omega™ Type T SLE thermocouples, with 24-gauge wire placed at opposite ends of the external bath at depths of 2.5 cm and 12.5 cm. In a limited number of trials, bath temperature was maintained as low as –12 C to determine the lower limit of supercooling.

Once tubers cooled to desired temperatures or when an exotherm occurred, the bath temperature was warmed at the rate of 1 C per hour. When tuber temperature reached 0 C, columns were removed from the bath and placed at room temperature. When tuber temperature reached 20 C, tubers were removed, washed, air-dried, and then stored in a dark germination chamber at 25 C to promote sprouting. After 10 days at 25 C, the number of viable eyes per tuber was recorded. Viable eyes were defined as those in which sprouts were beginning to develop. At least four tubers were tested for each temperature/exposure combination. All tests were repeated in time and data presented are representative output from individual trials. Tuber viability data were subjected to analysis of variance and treatment means were separated by the Duncan's NMRT at the 5% level.

Freezing Dynamics in Hydrated Soil Columns

Potato tubers, soil columns, and thermocouples were prepared as stated previously for air dried soil columns. Tuber weight averaged approximately 32 g within the size range reported for volunteer tubers in fields surveyed in south-central Washington State (Newberry and Thornton 1999). Single-distilled reverse osmosis water was added to bring the soil water content (SWC) to 7% (mass). The completed columns containing tubers were placed in a 2.0 C germination chamber for 24 to 36 h before testing to allow equilibration of column soil temperature. Five columns were placed in the ethylene glycol bath and the RTE140 was programmed to initially stabilize the soil temperature in all columns to 1.0 C, and then reduce the bath to a target temperature at a rate of 1.0 C per hour. To simulate field conditions where extensive supercooling of soil water does not occur (Spaans and Baker 1993), hydrated soil columns were artificially inoculated by placing a distilled water ice cube, 5 cm by 5 cm, on the soil surface when temperatures at the tuber center depth averaged about –1 C.

Once target temperatures or exotherm events were observed, the bath temperature was warmed at the rate of 1 C per hour. Columns were removed from the bath when tuber temperature reached 0 C and were placed at room temperature. When tuber temperature reached 20 C, tubers were removed, washed, inspected, air-dried, and then placed in a dark germination chamber at 20 C to promote sprouting. At 5 weeks after treatment, overall tuber condition was recorded, viable eyes were counted, and sprouts greater than 5 mm in length measured and recorded. At least five tubers were tested for each temperature/exposure combination. All tests were repeated in time and data presented are representative output from individual trials. Tuber mortality and sprout length data were subjected to analysis of variance and treatment means were separated by the Duncan's NMRT at the 5% level.

Exposure Time Studies in Hydrated Soil Columns

Individual tubers placed in hydrated soil (7% SWC) columns were exposed to –1.0, –1.5, and –1.9 C for 0, 2, 4, 8, 12, and 24 h. When the average soil temperature of all columns reached the target temperature, the RTE140 was programmed to maintain bath temperature at the target temperature for the appropriate interval. At the end of that time, the coolant temperature was raised 1.0 C per hour to 1.0 C, maintained at 1.0 C for 6 h before raising the bath temperature to 10 C over 9 h. Columns were then removed from the bath and allowed to stand at room temperature for at least 1 h. Tubers were removed from columns and tuber viability was evaluated as previously described for hydrated soil columns.

Field Studies

Survival of potato tubers buried at various depths in the field was evaluated in six winters from 1993 to 1999. Whole seed tubers of Russet Burbank were buried in November 1993, 1994, 1995, 1996, 1998, and 1999 at 5- or 7-cm-depth increments to a maximum depth of 20 cm (Table 2). Fields were left fallow the duration of the experiment. Trials were located in 1993, 1994, and 1999 at Paterson, WA, on a Quincy sand; 1994, 1995, 1996, 1998, and 1999 at Prosser, WA, on a Warden silt loam; and in 1999 at Othello, WA, on a Shano silt loam. In all trials, at least 20 tubers were buried each year at each depth and site. In most years tuber weight was 150 to 200 g, within the weight range of tubers left after potato harvest. Two or more type T thermocouples (Omega™) were buried in each plot at the depth of the center of tubers to record soil temperature. Single junction thermocouples insulated with adhesive filled heat-shrink tubing were multiplexed to a Campbell Scientific™ AM416 and data was recorded on a Campbell Scientific™ CR10 data logger. In

1998 and 1999, smaller tubers averaging 50 g were used and one half of the plots were seeded to winter wheat at 110 kg ha^{-1} and the other half left fallow in a split plot design with four replications.

For trials conducted between 1994 and 1997, tubers were recovered in the spring and viability determined by placing them in the dark at 20 C and counting the number of developed sprouts for 8 weeks. In 1999 and 2000, tubers were not removed from the soil and tuber viability was determined by counting the number of emerged shoots in April, May, and June. Tuber mortality and viability data were subjected to analysis of variance and treatment means were separated by the Fisher's least significant difference at the 5% level.

RESULTS AND DISCUSSION

Freezing Dynamics in Air-dried Soil Columns

After placing soil columns containing tubers in the ethylene glycol bath, potato tuber temperature dropped steadily and most tubers supercooled to a temperature of –3 to –7 C before an exotherm occurred (Figure 1). Most plant tissues supercool several degrees due to a lack of nucleating substances necessary for ice initiation or ice growth barriers present in some tissues (Burke et al. 1976). Nucleation temperature varied substantially between tubers, which supports the findings of several researchers studying freezing characteristics of tubers in air (Cunningham et al. 1976; Jones et al. 1919; Wright and Diehl 1927). Exotherms varied as much as 10 h apart in the same test (data not shown). When tubers froze, a distinct exotherm occurred resulting in a rapid rise in tuber temperature, which stabilized at about –1.4 to –1.5 C (Figure 1), then continued to drop until stabilizing at the ambient temperature of the ethylene glycol bath. The stabilization of tuber temperature at –1.4 to –1.5 C was interpreted as the actual freezing point of the tuber and the associated low-temperature exotherm representing the latent heat of freezing (Proebsting and Andrews 1982).

Subsequent experiments were conducted in which tubers were removed from columns at various times relative to an exotherm event. All tubers that underwent an "exothermic event" (Wiest and Steponkus 1978) reaching –1.4 C for brief periods of 1 to 2 min before warming columns and removing from the bath were unable to sprout and were visually damaged. Tuber freezing damage consisted of leakage of fluids and tubers lacked firmness, becoming soft and pliable. Generally, the stabilization in temperature following an exotherm lasted between 1 and 3 h. All tubers that had not undergone an exotherm, but supercooled well beyond the anticipated freezing point were able to sprout, even when held at –3 C for 48 h or at –4 or –5 C for 12 h (data not shown). Cunningham et al. (1976) reported much variability in the degree of supercooling of tubers within the same lots. Previous researchers reported that the extent to which potato tubers supercool is dependent upon the temperature at which they are previously stored and the rate of cooling, although there is little variation in the actual freezing point (Levitt 1980; Wright and Diehl 1927; Wright and Taylor 1921).

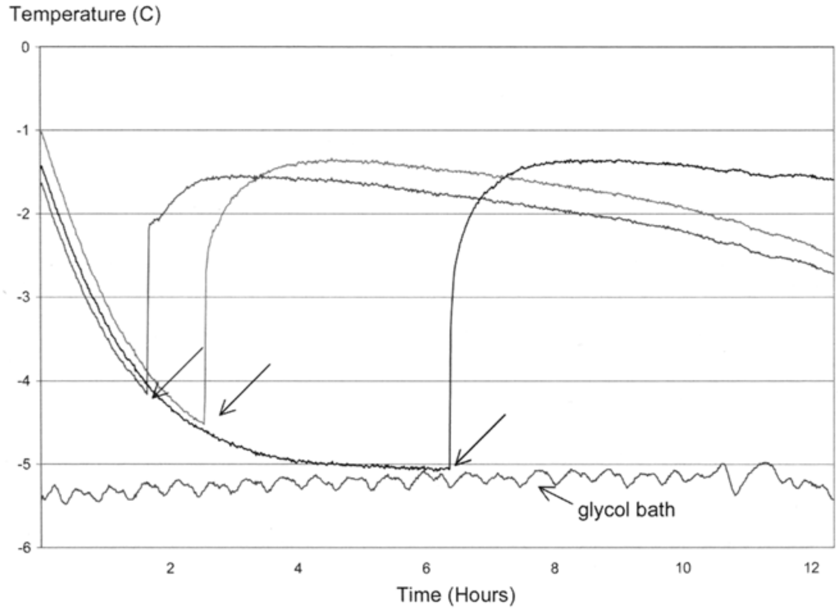

FIGURE 1.
Supercooling and exotherms of three potato tubers in air-dried soil columns subjected to cold temperatures. Arrows indicate exotherms occurring at 1.6 h, 2.5 h, and 6.3 h, characteristic of the variation observed among all tubers tested.

Freezing Dynamics in Hydrated Soil Columns

Soil columns hydrated to 7% SWC experienced an initial exotherm generally when soil temperatures reached –1.6 to –1.7 C. In initial experiments, the ice nucleation tem-

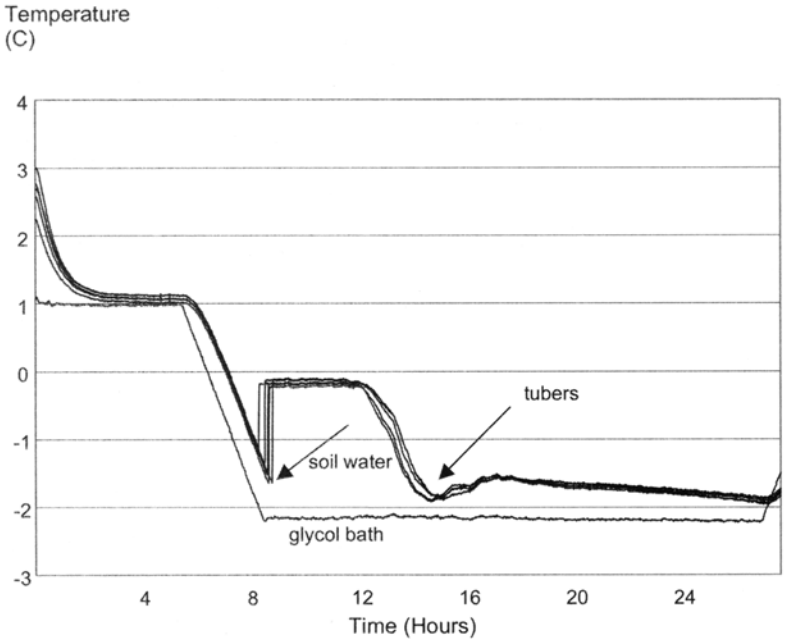

FIGURE 2.
Exotherms of five potato tubers in hydrated soil columns (7% SWC) subjected to cold temperatures. Initial exotherms (marked with arrow) represents freezing of soil water and second exotherm (marked with arrow) represents tuber freezing.

TABLE 1—*Potato tuber sprout length (cm) after 5 weeks at 20 C following exposure to three soil temperatures in hydrated soil columns for specified times. Dashes indicate not tested*

Soil Temperature (C)	Exposure Time (h) 0[1]	2	4	8	12	24
–1.9	4.7 b[2]	2.8 b	–	–	0.0 c	–
–1.5	9.5 a	–	4.9 b	4.7 b	4.4 b	1.3 c
–1.0	13.0 a	–	8.4 a	10.6 a	14.2 a	12.3 a
Nontreated	14.3 a	–	–	–	–	–

[1]For zero exposure times, soil columns containing tubers were warmed immediately when target temperature was reached.
[2]Means followed by the same letter are not significantly different according to Duncan's multiple range test at the 5% level.

perature for this exotherm was somewhat variable. In subsequent experiments, the variability was reduced by placing an ice cube on the surface of the soil column to artificially inoculate the column. During this initial exotherm, temperature stabilized briefly at –0.3 C before continuing to drop (Figure 2). This exotherm likely represents freezing of the soil water (extracellular freezing). Alternatively, this exotherm may represent the intercellular freezing of water in the tuber tissue, but a similar exotherm was not encountered in tubers in dry soil leading us to believe that this represents the soil water freezing.

A second exotherm occurred with tuber temperature stabilizing at –1.9 C (Figure 2). Tuber temperature often reached –2.0 to –2.2 C, before the second exotherm took place. All tubers warmed and removed prior to experiencing this second exotherm were viable, whereas all tubers that were warmed immediately after undergoing this exotherm were nonviable. This second exotherm was interpreted to represent the freezing of intracellular water, which occurs at a lower temperature than the first exotherm due to the solute content of the cells (Sutcliffe 1977; Walker 1952). The stabilization of temperature following the second exotherm lasted about 4 to 7 h. The rate at which the heat of fusion dissipates depends on the mass of the tuber and thermal diffusivity of the surrounding medium, which varies with soil water content for a given soil at a given bulk density (Ashworth et al. 1985b).

The difference in ice-nucleating temperatures of tubers in dry soil compared to tubers in moist soil suggests that ice-nucleating particles active at higher temperatures are associated with the moistened soil. In hydrated soil, soil ice was likely able to nucleate the tuber tissue through lenticels or wounds, and the tubers were not able to supercool to the degree of tubers in dry soil. The greater extent of supercooling of tubers in dry soil compared to tubers in moist soil was likely not due to any minor changes that may have occurred in the turgidity of the potato tubers.

The actual freezing temperature of potato tubers probably falls between –1.4 and –1.9 C, the stabilized temperatures following exotherms in air-dried and hydrated soils, respectively. This is the first report of the freezing point of potato tubers in a soil medium. These results are in agreement with those of previous researchers working with tubers not exposed to soil (Jones et al. 1919; Link and Ramsey 1932; Maximov 1914; Wright and Diehl 1927; Wright and Taylor 1921), which concluded that the freezing point of potato tubers was near –1.6 C.

Time of Exposure in Hydrated Columns

Tubers exposed to temperatures near the freezing point (–1.4 to –1.9 C) in hydrated soil columns for periods of 1 min to 24 h, but not allowed to experience an exotherm exhibited varying degrees of injury. Tubers held at –1.0 C for 4 to 24 h were able to sprout similar to nontreated control (Table 1). Tubers held for a very brief period of time at –1.5 C sprouted normally, but when held at –1.5 C for periods of 4 h or more, sprout development was retarded. Tubers held at –1.5 C for 12 h or more leaked fluids when removed from soil columns, and sprout development was severely hindered. Some tubers exposed to –1.9 C for 1 min and up to 2 h were able to produce some weakened sprouts, but 30% of the tubers were dead. All tubers held for 12 h at –1.9 C were nonviable.

FIGURE 3.
Potato shoots sprouting from the lower surface of tubers in which the upper surface was exposed to soil temperatures near –1.9 C.

Lumkes and Sijtsma (1972) reported that temperatures above –2.0 C had no freezing effect upon tubers. These results indicate that the viability of potato tubers was reduced at temperatures between –1.5 C and –1.9 C, with injury increasing as time of exposure was lengthened. Applying the Lumkes and Sijtsma formula to the data significantly underestimates the extent of tuber mortality, and although the required 50 h below –2.0 C was not accumulated there was a significant reduction in tuber viability. Cunningham et al. (1976) reported extensive symptoms of chilling injury to tubers held at –2.5 C for 29 h or –3.8 for 10 h; whereas tubers held at –1.1 C for 80 h had very little injury. However, tuber viability and sprouting were not measured in those studies.

Field Trials

Winter soil temperatures increased with soil depth and temperature differences between depths were greatest during cold events (Figure 4). In five of six winters, few or no tubers survived when buried with only 5-cm soil cover (Table 2). In the winter of 1999 to 2000, soil temperatures at the 5-cm depth fell below 0 C only at the Othello site, which reached –2.0 C and did not significantly reduce subsequent sprout emergence (Table 2) compared to deeper tubers which remained warmer. Among all burial depths, sites, and years, whenever minimum soil temperature reached –2.8 C or colder, significant tuber mortality occurred (Table 2). When minimum soil temperature at the depth of the center of tubers buried 5 cm was lower than –2.8 C, no tubers survived.

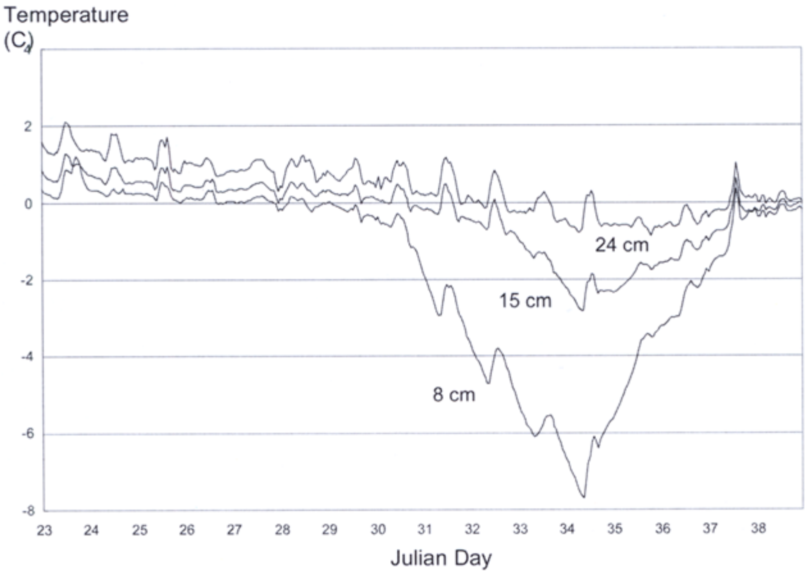

FIGURE 4.
Soil temperatures measured by thermocouples placed at 8, 15, and 23 cm depth near Prosser, WA, 26 January through 9 February 1996.

In 1993-94, 93% of tubers buried 20 cm deep where minimum soil temperatures were –1.5 C were viable. In 1994-95 at the Paterson site, 88% of tubers buried 13 cm deep where minimum soil temperatures reached –1.9 C were viable compared to 100% viability of tubers buried 20 cm deep where minimum temperatures were –0.5 C (Table 2). In 1994-95, substantial freezing injury occurred on the upper portion of tubers buried at 13 cm at both sites, affecting 7% of the

TABLE 2—*Winter survival of potato tubers buried at various depths in autumn and minimum soil temperatures recorded at tuber depth from 1993 through 1999 in the Columbia Basin of Washington. Fields were left fallow the duration of the experiment.*

Year	Location	Tuber Depth[1](cm)	Percentage Survival[2] (%)	Minimum Soil Temperature[3](C)
1993-94	Paterson	5	0 b	−6.0
		20	93 a	−1.5
1994-95	Prosser	5	4 b	−2.8
		13	100 a	−1.1
		20	100 a	−0.3
	Paterson	5	0 c	−4.5
		13	88 b	−1.9
		20	100 a	−0.5
1995-96	Prosser	5	0 c	−7.7
		13	45 b	−2.8
		20	98 a	−0.8
1996-97	Prosser	5	0 c	−4.3
		10	0 c	−3.6
		15	88 b	−1.5
		20	100 a	−0.1
1998-99	Prosser	5	0 b	−6.2
		10	0 b	−4.8
		20	98 a	−0.7
1999-00	Prosser	5	95 a	≥0.0
		10	97 a	≥0.0
		15	77 a	≥0.0
		20	75 a	≥0.0
	Paterson	5	96 a	≥0.0
		10	98 a	≥0.0
		15	90 a	≥0.0
		20	86 a	≥0.0
	Othello	5	70 a	−2.0
		10	79 a	≥0.0
		15	70 a	≥0.0
		20	64 a	≥0.0

[1]Depth of soil cover above upper surface of tuber.
[2]1993-1996 percentage survival = number of recovered tubers able to produce a sprout in the dark at 20 C divided by the total number of tubers planted × 100. 1998-2000 percentage survival = number of tubers with emerged sprouts in late May to early June divided by the number of tubers planted × 100. Means within a site and year followed by the same number are not significantly different according to Fisher's protected least significant difference at the 5% level.
[3]Minimum soil temperature at depth of tuber center.

tubers at Prosser and 30% of the tubers at Paterson, indicating soil temperatures at the 13-cm depth were near the critical point for tuber survival (Figure 3). This phenomenon was also evident in 1995-96 for tubers buried 13 cm, which reached a minimum soil temperature of −2.8 C. More than half the tubers at this depth were unable to sprout, but 12% of the tubers were able to develop sprouts on the lower portion of the tuber despite freezing injury on the upper tuber section. Soil temperatures were recorded at the depth of the center of the tuber, and the temperature on the upper surface of tubers was undoubtedly lower as the result of the thermal gradient of the soil. Once ice nucleation occurs, the advancing ice front will spread until it reaches water that is above the freezing point, and then stop propagating (Fuller and Wisniewski 1998).

In 1996-97, 12% of tubers buried 15 cm deep, where minimum soil temperatures reached −1.5 C (near the tuber freezing point), were killed. Another 60% of the tubers buried 15 cm deep exhibited freezing injury on the upper tuber surface although sprouts developed on the lower tuber surface. These data support the laboratory results, which indicate that potato tubers suffer irreversible damage when exposed to soil temperatures near −1.5 to −1.9 C or lower for brief periods. In 1998-99, all tubers at the two shallow depths of 5 and 10 cm died after exposure to −6.2 and −4.8 C, respectively, whereas 98% of the tubers at 20 cm depth survived where minimum temperatures reached only −0.7 C.

In field studies, cooling rate of soil surrounding tubers ranged from 0.05 to 0.12 C per hour during freezing events depending on soil depth. The rate of tuber cooling was more rapid in soil column studies and may affect the degree of injury to the tubers. Levitt (1980) reported potato tubers are unable to harden and could be maintained indefinitely at 0 to 5 C without suffering injury or altering their resistance to freezing. In contrast, Walker (1952) reported the freezing point of potato tubers is generally lowered by about 1 C when tubers are held at low temperature near 1 C for extended periods.

The effect of growing a cover crop of winter wheat vs no cover crop on soil temperature and survival of volunteer potatos was investigated in 1998-99 and 1999-00. In 1998-99, minimum soil temperature at 10- and 20-cm depths ranged from 0.3 to 0.9 C warmer beneath a winter wheat cover crop than with no cover crop (data not shown). All tubers buried at depths of 5 cm and 10 cm died as minimum soil temperatures reached −4.2 C or lower (Table 3). By 27 May 1999 sprouts emerged from 82% of tubers buried at 20 cm in winter wheat

TABLE 3—*Potato sprout emergence on 27 May 1999 and minimum soil temperatures recorded at tuber depth in 1998-99 from tubers buried at three depths in autumn in plots planted to winter wheat[1] or left fallow at Prosser, WA.*

Tuber Depth[2](cm)	Minimum Soil Temperature[3] (C) Fallow	Winter Wheat	Sprout Emergence[4](%) Fallow	Winter Wheat
5	−6.2	−6.5	0 c	0 c
10	−4.8	−4.2	0 c	0 c
20	−0.7	−0.4	93 a	82 b

[1]Winter wheat planted 14 October 1998

[2]Depth of soil cover above upper surface of tuber.

[3]Minimum soil temperature recorded at depth of tuber center.

[4]Percentage sprout emergence = number of tubers with emerged sprouts 27 May 1999 divided by the number of tubers planted × 100. Means followed by the same number are not significantly different according to Fisher's protected least significant difference at the 5% level.

cover plots compared to 93% emergence from tubers buried 20 cm in fallow plots. Sprout emergence from winter wheat plots was delayed possibly due to slower warming of soil or lower soil moisture in the wheat cover crop although soil temperatures were not monitored past late March. In 1999-2000, growing a wheat cover crop did not affect total emergence of potato sprouts in early June, but delayed sprout emergence in early May (data not shown). Other researchers have reported that autumn-sowed wheat delays emergence of volunteer potatoes (Aarts and Sijtsma 1978; Lutman 1974) and reduces total potato emergence (Newberry and Thornton 2004; Thomas and Smith 1983). Delayed potato emergence in those studies was attributed to lower soil temperatures under wheat residue compared to fallow. Given that the majority of tubers left after potato harvest are shallow in the soil profile, small changes in the depth of penetration of lethal temperatures could have major impacts on the numbers of surviving tubers.

Some potato fields are tilled and planted to a cover crop following harvest, while many fields are left untilled post-harvest. Surface residues such as mulches or cover crops behave as insulators, moderating environmental conditions in the soil (Bristow 1983). The presence of a cover crop would tend to modify the extremes in soil temperatures and also to accumulate more snow cover, which acts as an excellent insulator (Carson 1961). Conversely, bare soil would tend to allow for deeper penetration of lethal temperatures following cold events. Tillage may also alter the thermal diffusivity of the soil and allow for deeper penetration of lethal cold temperatures (Carson 1961).

Tubers left in the field following potato harvest can vary greatly in size. The effect of tuber size on freezing behavior was not extensively evaluated in these studies. Tubers of slightly different sizes were used in various years of field studies, but direct comparisons of survivability based on tuber size between years cannot be made statistically. When tuber size was included as a variable within a trial little or no differences in winter survival were observed (data not shown). Under field conditions with extensive numbers of nucleation sites, little or no supercooling would be expected, and the effect of tuber size is probably negligible. Tuber size likely influences shoot vigor, ability to emerge from deeper depths, and ability to recover from various control treatments more than winter survival.

CONCLUSIONS

These data support empirical observations that potato tubers at shallow depths are much more likely to be subjected to lethal cold temperatures than tubers at deeper depths. In 5 of 6 years of the trials reported here, greater than 90% of tubers buried 20 cm deep survived, whereas in 5 of 6 years, tubers buried only 5 cm deep were subjected to lethal temperatures. In the Columbia Basin potato-producing region of Washington and Oregon, air temperatures during the winters of 1993 to 2000 were seldom cold enough to allow lethal temperatures to occur deeper than 10 cm the soil profile. Growers can increase the likelihood of tubers being subjected to lethal temperatures by eliminating fall tillage practices that bury tubers deeper.

Monitoring soil temperatures at various depths could allow forecasting of problems with volunteer potatoes in the ensuing cropping season. Based on the results of these studies, when minimum soil temperatures reach −2.0 C at tuber depth for brief periods tuber mortality occurs. Mortality of tubers was greater than would be predicted by the model of Lumkes and Sijtsma (1972), which required 50 h accumulated below −2 .0 C before tuber death. Soil temperatures monitored at various depths could be coupled with estimates of tuber leavings by depth, allowing for reasonable predictions of the volunteer potato problem. Tuber populations at various depths in the soil have been documented following various fall tillage practices (Newberry and Thornton 1999). Minimum temperatures throughout the soil profile can be modified by the amount of residue cover, snow cover, and soil moisture content. Therefore, monitoring of soil temperatures by depth would be most useful in predicting volunteer potato mortality when done in close proximity and in fields with similar amounts of residue and snow cover as the fields where volunteer potatoes are being managed.

Monitoring soil temperatures could also allow for fall and winter tillage practices to be tailored for maximum exposure of tubers to freezing temperatures. For example, if soil temperatures in the upper 16 cm of soil reached -2.0 C or colder late in the fall or early winter, resulting in death of tubers in the upper profile, the soil could be plowed to expose deeper buried tubers to lethal temperatures occurring later in the winter (Thomas and Smith 1983). In extremely mild winters or extremely cold winters, the tuber distribution by depth has little influence on tuber survival. However, in winters where occasional freezing events occur and lethal temperatures reach only several centimeters deep in the soil profile, tillage practices in the fall that bury tubers deeper in the profile could greatly increase the number of surviving tubers.

Most plant tissues are able to supercool regardless of their hardiness (Burke et al. 1976). Supercooling probably occurs because of a lack of nucleating substances necessary for ice initiation. Under field conditions extensive supercooling of soil water is unlikely to occur due to numerous nucleation sites afforded by soil (Carson 1961; Spaans and Baker 1993). These studies did not attempt to measure supercooling of tubers in field situations. However, in hydrated soil columns, only slight supercooling of tubers was observed. Soil ice in hydrated columns could have provided nucleation sites to catalyze ice formation at higher temperatures in the tubers. Soils in natural field settings would likely resemble the hydrated soil columns used in these studies, in which limited supercooling occurred.

Under field conditions, the temperature of the tuber would not likely be as uniform as in a laboratory setting due to the thermal gradient in the soil profile, and as a result, tubers in field situations would be less likely to supercool. In field trials where tuber freezing injury occurred, the upper surface of tubers was often killed while the lower surface remained unharmed, whereas tubers in laboratory soil columns were not injured differentially on one side of the tuber.

Although differences in freezing behavior of potato tubers in dry vs hydrated soil were observed, it is unlikely that soil in field situations could reach the dryness obtained in dry soil columns used in these studies. Hydrated soil columns would more closely resemble soil water contents encountered in field situations. The temperature of moist soil fluctuates less than dry soil due to the high heat capacity of water relative to soil and air. Wet soils are better heat conductors and able to store more heat than drier soils. As a result, tubers in drier soil would be more likely to experience lethal temperatures.

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